Z. Säugetierkunde **63** (1998) 321–328

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Individual migration between colonies of Greater mouse-eared bats (*Myotis myotis*) in Upper Bavaria

By A. ZAHN

Zoologisches Institut, Universität München, München, BRD

Receipt of Ms. 12. 01. 1998
Acceptance of Ms. 21. 04. 1998

Abstract

Dispersal between 22 nursery colonies of *Myotis myotis* was studied in Bavaria (Germany) from 1991 to 1993. Each year 6–7% of the observed banded females settled in colonies other than the one where they had been banded and short visits of females to other colonies were also observed. Movements occurred over a distance up to 34 km. Emigration rates in reobserved bats varied between colonies from 0 to 25%. In some cases, emigration did not seem to be spontaneous but may be caused by environmental factors such as unfavourable climatic conditions at the roost.

Key words: *Myotis myotis*, dispersal, emigration, cave bats

Introduction

Central European females of *Myotis myotis* form nursery colonies in attics between April and August while adult males live separately at individual roosts. Observations of banded individuals showed that movements between colonies occurred up to a distance of about 30 km and that 3 to 26% of all recaptured females migrated to other colonies (EISENTRAUT 1960; FELTEN and KLEMMER 1960; HAENSEL 1974; HANÁK 1989; HORÁCEK 1985; HURKA 1988; OLDENBURG and HACKETHAL 1989; ROER 1968, 1988). However, these observations do not indicate whether the controlled sample was representative of the studied population, and roost sites were not observed systematically. As a result it is not known how many migrants were only brief visitors to the alien colonies and how many were permanent settlers. Also it is unknown whether bats moved spontaneously or whether movements were triggered by external events. Casual observations suggest that bats may move to an alternative roost, if they are disturbed by predators, e. g. martens or owls (HENKEL et al. 1982; MÜLLER et al. 1992; ROGÉE and LEHMANN 1994).

Furthermore, banded individuals are easily overlooked in sporadic observations because bats are frequently absent from the colony for several days (BILO 1990; BRAUN 1989; GEBHARD and OTT 1985; RUDOLPH and LIEGL 1990). This may be especially true for one-year-old non-reproductive females (HORÁCEK 1985; ZAHN 1995). Also, banded bats might disappear by mortality and emigrants may not move to all neighbouring colonies to the same extent. To estimate the emigration rate (versus mortality) all colonies within an area have to be observed systematically.

Some authors report that the number of movements declines with increasing distances between colonies (GAISLER and HANÁK 1969; HAENSEL 1974; HORÁCEK 1985) but other factors might additionally influence immigration rate: Females may meet bats of other colonies in the foraging areas and follow them to their roosts. If this is the case, larger colonies should be known to more members of a population than smaller colonies, since the probability of meeting a member of a given colony rises with its size. In larger colonies, therefore, more immigrants and visitors should be observed than in smaller ones. However, because the probability of movements between colonies decreases with increasing discance, both size and distance must be considered.

To determine the extent of movements (emigrations, visits) between colonies the presence of banded females in 22 nursery roosts was observed in this study. Moreover, the effects of colony size and distances on immigration rate were analysed.

Material and methods

The study was conducted from 1991 to 1993 in an area of 4 000 km^2 located in the south-eastern part of Upper Bavaria, (between Munich and lake Chiemsee) where 22 nursery colonies exist (Fig. 1). Probably all colonies of the area were known because of intensive reconnaissance of potential roosts (Zahn 1995). Bats were banded in three colonies settling in churches of the villages Au (colony size 700 adult bats), Litzldorf (45 adult bats) and Beyharting (200 adult bats). Banding began between 1987 and 1990 (Audet 1992; Vogel pers. comm.) when 214 nursing or juvenile females were marked in Au and Litzldorf. 116 juvenile females of Au and 53 of Beyharting were banded shortly before weaning (end of July, beginning of August) in 1991. Additionally, 44 adult and 8 juvenile females were banded during the mating season in August and September (Zahn and Dippel 1997). Altogether, 435 females were banded in the area. The total number of females in the area was about 3 000–4 000 (Zahn 1995). While females had been banded with two or three coloured plastic rings (Audet 1992) in the previous studies, one aluminium ring (ZOOL. MUSEUM BONN) per bat was used in 1991 to follow new banding regulations. Differently coloured spots of reflective tape were fixed to the aluminium rings to identify the bats over a distance of about 2 m. Plastic rings could be identified from a distance of 3 m. 15 of the 22 nursery colonies were visited two to four times a month between May and August in 1991, 1992, and 1993. The seven remaining colonies of the study area were visited one to three times each summer. All other colonies of Upper Bavaria were checked once a year (end of July, beginning of August).

Individuals that had left their birth colony and were observed in their new colony for several times during pregnancy and parturition were considered as "emigrants". Bats that were observed only once in another colony were classified as "other migrants". "Other migrants" includes bats that were never seen again after the observation and others that were found again at the banding site after their visit to another colony.

For correlation analyses Kendall's Tau was used. To analyse whether larger colonies are known to more members of the population than smaller ones and to determine the influence of the migration distance, the following partial correlations were calculated (Zöfel 1992): correlation between the number of "immigrants plus other migrants" in a colony and its size (distance mathematically constant) and correlation between the number of "immigrants plus other migrants" in a colony and the distance of the colony where the "immigrants/other migrants" had been banded (colony size mathematically constant).

It was not possible to determine the origin of 5 migrating bats (Au or Litzldorf) that had lost plastic rings or chewed off parts of the reflective tape. Therefore data of Au and Litzldorf were combined to include these cases into the correlation analyses. A point located at half the distance between both villages (7 km) was regarded as the origin of the individuals. Therefore, the distance a bat had moved can be over- or underestimated up to 3.5 km.

Additionally data from Bohemia (Czech Republic) published by Horácek (1985) were analysed. He gives the number of emigrants from the colony at Beroun that were found in five other colonies. The colony sizes, the distances to Beroun, and the numbers of migrants were (size-km-number): 250-16-11, 150-4-9, 70-8-4, 50-11-4, and 40-25-1.

Results

Reobserved bats

170 of all 435 marked females were observed at least once during the years after banding. The majority of them (84%) was resident at the banding site. However, 27 (16%) of the 170 bats were found in colonies different from those where they had been marked. Fourteen (52%) of them were "emigrants" and thirteen "other migrants". Eleven of those "other migrants" were found in alien colonies before the period of parturition.

For 22 of all 27 bats (nine "other migrants" and 13 "emigrants"), it was possible to identify the colony where they had been banded. Eight females were marked in Beyharting, eight in Au, and six in Litzldorf (Fig. 1). The remaining five bats were observed in colonies where no bats had been banded but the banding site (Au or Litzldorf) could not be specified. Bats had moved as far as 34 km (two specimens) with the remaining bats moving between seven and 30 km. The average distance was 15 km.

During each year of the study, 6% to 7% (5–9 individuals) of all observed banded females lived permanently in another colony than the one in which they had been marked. 4% to 7% (3–9 individuals) of banded bats were observed as "other migrants" in other colonies each year.

The percentage of emigrated females among the 170 bats recovered in the years after banding was much lower in the large colony of Au than in the smaller colonies of Litzldorf and Beyharting (Tab. 1).

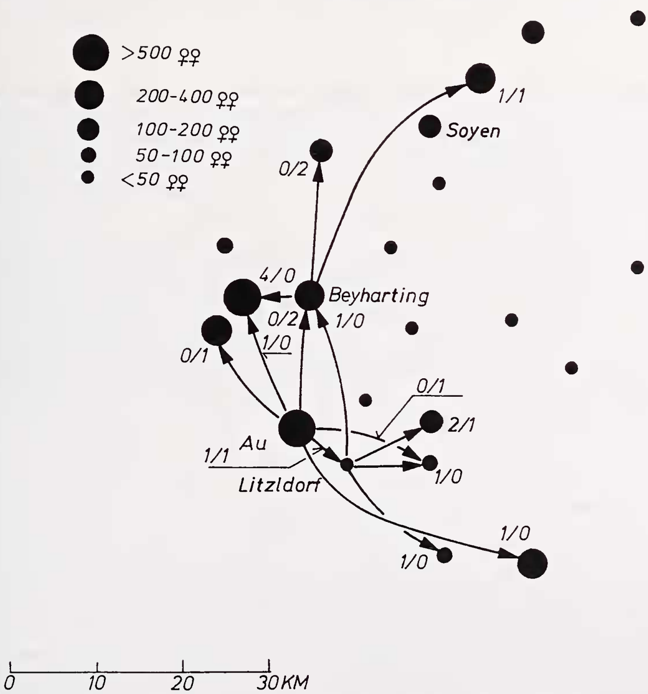

Fig. 1. Movements between colonies of *Myotis myotis* in the study area in Bavaria (1991–1993). All colonies of the area are marked by a circle. The banding sites are indicated by the names of the villages Au, Beyharting, and Litzldorf. The colony at Soyen where the emigration of many unbanded bats was observed is also named. The size of the colonies (number of adult females) is indicated by the size of the circles. The number of movements (immigrants/other migrants) is given beneath the arrows.

Table 1. Emigration rates in reobserved female *Myotis myotis* banded in the colonies Au, Beyharting, and Litzldorf. Size of the colonies: adult bats; n: number of reobserved individuals

colony (size)	emigrants in all bats recovered after banding	emigrants in the banded juveniles observed in 1992	emigrants in the banded juveniles observed in 1993
Au (700)	2% (n = 129)	0% (n = 48)	0% (n = 40)
Beyharting (200)	24% (n = 21)	24% (n = 21)	27% (n = 15)
Litzldorf (45)	25% (n = 20)	no juveniles banded	

Ten out of the 27 bats observed in other colonies (four "emigrants" and six "other migrants") were adult (>1 year) when they had moved between sites. In the case of nine bats banded before 1991, age at migration is unknown. Five "emigrants" and three "other migrants" moved within their first year of life. The five emigrants were born in the colony of Beyharting, suggesting that juvenile dispersal differed between Au and Beyharting (Tab. 1).

In 1993, when females born in 1991 were two years old and probably reproductive (Audet 1992; Horácek 1985), four of the five emigrated bats were still observed in their new colony. About 51 two-year-old bats settled at their banding sites (11 in Beyharting and about 40 in Au). Thus, 7% of all 55 banded two-year-old bats observed in 1993 had settled in alien colonies at the assumed beginning of their reproductive life.

Relationship between size of colony, distance of migration, and extent of immigration

The correlation analyses included all migrations from the banding sites to the neighbouring colonies within a distance of 34 km (Au/Litzldorf: 9 colonies, Beyharting: 10, Beroun: 5). All partial correlations between the number of "immigrants plus other migrants" and the size of the colony are positive (sample Au/Litzldorf: $r = 0.57$; sample Beyharting: $r = 0.46$; sample Beroun: $r = 0.96$), and all correlations between the number of "immigrants plus other migrants" and the distance from the colony, where the animals had been banded, are negative (sample Au/Litzldorf: $r = -0.70$; sample Beyharting: $r = -0.05$; sample Beroun: $r = -0.25$). However, only two of these correlations are significant ($p < 0.05$): The correlation between the number of emigrants from Beroun and the size of colony and the correlation between number of emigrants from Au and Litzldorf and distance of migration (Fig. 2 a, b).

Discussion

The majority of banded bats was not observed in subsequent years. Mortality might be much more important than migration to unknown sites in explaining their disappearance. Adult females settle permanently in colonies in summer, most colonies in the area are assumed to be known and no banded bats were found in other colonies in Upper Bavaria. The observed mortality rates in the studied colonies (59% for young and 22% for adult females, Zahn 1995) are consistent with results of Horácek (1985) and studies on other species (Findley 1993). However, some immigrants in the 7 colonies that were only visited one to three times each summer might not have been detected – especially one-year-old immigrants that are absent from colonies more often than older ones (Horácek 1985; Zahn 1995). Therefore, the emigration rate of banded individuals may be underestimated.

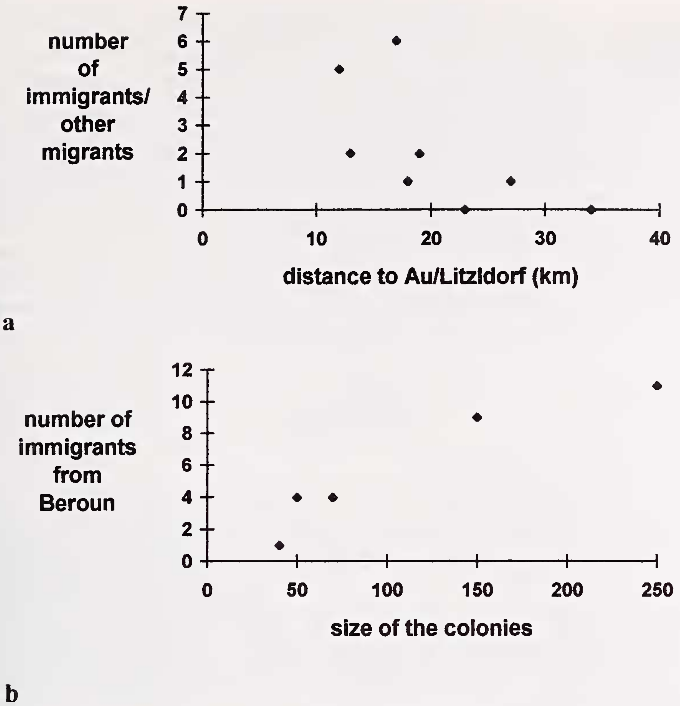

Fig. 2. Correlation between immigration, distance and, colony size.
a, correlation between the number of "immigrants and other migrants" in colonies of *Myotis myotis* and the distance to the site (Au/Litzldorf,) where the bats had been banded; r = 0.70. b, correlation between the number of "immigrants" in colonies of *Myotis myotis* and the colony size (banding site: Beroun; data from HORÁCEK, 1985); r = 0.96

It is also probable that more short stays of individuals in other colonies were made than observed. In the case of females banded after fledging movements may have been misinterpreted if an individual was just visiting a colony when it was caught to be marked.

Few females settled spontaneously in another colony. A reason for the high emigration rate in Litzldorf might be the cold spring in 1991. The colony disappeared in May during a spell of cold weather which might have affected this site much more than others, due to the cool temperatures of the attic (in Litzldorf the lowest average spring roost temperature of 10 colonies settling in churches was measured (ZAHN 1995)). Some banded bats, which later returned, were observed in neighbouring colonies during the cold period (AUDET 1992). In June, about 40% of the colony had returned. The remainder are assumed to have settled in neighbouring colonies, because banded emigrants were observed in four of them. Climate of the roost might have caused emigration also in the colony at Soyen church (160 adult bats), located in the northern part of the study area (Fig. 1), where the highest roost temperatures of all colonies were measured (ZAHN 1995). Temperatures in the church tower where the bats roosted exceeded regularly the preferred temperature range of *Myotis myotis* (HEIDINGER et al. 1989; ZAHN 1995). In May 1993, which was extremely hot, this colony disappeared. The bats had no traditionally used roost in cooler places of the building, as other colonies (which used such sites during this time). During a cooler period in June, 65% of the bats returned. However, because no bats had been banded in Soyen, it cannot be verified that the missing females had settled in neighbouring colonies.

In 1991 there was a striking difference in the dispersal rates of young bats banded in Au and Beyharting. While the colony size of Au (no emigrants) was constant during the study, the colony Beyharting declined by 25%. About the same percentage (27%) of the females banded in Beyharting and still living in the area in 1993, settled in other colonies. This indicates not spontaneous movements of individual bats, but a long term emigration of parts of the colony in Beyharting for unknown reasons (food shortage was probably not the reason for emigration: the other colonies within the potential foraging area of 15 to 25 km (Arlettaz 1995) of the Beyharting bats did not decline or increased). Spontaneous dispersal of juvenile females seems to be very low as indicated by the bats of Au.

Females visit neighbouring colonies up to a distance of about 30 km sporadically and may settle in the foreign colony if unfavourable conditions occur at their site of birth. As in studies of Roer (1968) and Audet (1992) most short visits of bats to alien colonies were observed before the period of parturition. The maximum observed migration distance of 34 km somewhat exceeds the maximum observed distance (25 km) between colonies and foraging areas (Arlettaz 1995). The results of the correlation analyses suggest that larger colonies tend to receive more immigrants and that there is a higher exchange of individuals between closer colonies.

In southern Europe *Myotis myotis* is a perennial cave-dwelling species. A low dispersal rate may be characteristic for cave-bats. Tuttle (1976) found only 1% of female *Myotis grisescens* in home ranges of other colonies. Female *Miniopterus schreibersi* visit other colonies but all of them give birth in the colony where they were born (Palmeirim and Rodrigues 1995). *Miniopterus* and *Myotis myotis* need no dispersal to avoid inbreeding: individuals from different colonies meet at the mating sites (Palmeirim and Rodrigues 1995; Zahn and Dippel 1997). Palmeirim and Rodrigues (1995) expect strong philopatry to evolve when colonies are large and when the rate of colony extinction is low, which is the case in *Miniopterus* since caves provide ever-lasting roosts.

Because of their long time existence all caves suitable for a cave-bat species should have been colonised and occupied by the maximal number of bats which the local resources may support. Therefore, Audet (1992) expects that the average fitness of individuals should be equal in different colonies (if basic conditions as e.g. climate do not change), and that no bat can improve its fitness by moving to another colony. This may also cause the low dispersal rates in cave bats.

Buildings are less durable roosts with less constant conditions than caves. This could explain the more frequent movements in the Bavarian population of *Myotis myotis* compared to *Myotis grisescens* and *Miniopterus*. However, *Myotis myotis* settles in central European attics only since the past few hundred years. This period seems too short for an evolution of higher dispersal rates and therefore this species may keep the potential to disperse also in other areas. Studies on dispersal in south European populations could show whether dispersal patterns changed when this species extended its distribution range to the north.

Acknowledgements

I am indebted to Prof. G. Neuweiler, Dr. K. Richarz, C. Liegl, A. Liegl, Dr. D. Friemel, and A. Schumm for their suggestions and valuable contributions to the conception of the study. Prof. G. Neuweiler and M. Meinl read earlier drafts of the manuscript and offered many helpful comments. I thank Prof. T. Park, J. Harrison, and U. Ludwig for help with the translation and H. Zahn for preparing figure 1.

Zusammenfassung

Individuenaustausch zwischen Kolonien des Großen Mausohrs (Myotis myotis) in Oberbayern

Von 1991 bis 1993 wurde die Anwesenheit beringter Mausohren (*Myotis myotis*) in 22 Kolonien eines bayerischen Untersuchungsgebiets bei regelmäßigen Quartierkontrollen überprüft. In jedem Jahr siedelten 6–7% der beobachteten Tiere in einer anderen Kolonie als in jener, in der sie beringt worden waren. Auch wurden Kurzbesuche beringter Tiere in Nachbarkolonien festgestellt. Überflüge fanden in bis zu 34 km weit entfernte Kolonien statt. Betrachtet man alle nach der Beringung wiedergefundenen Tiere, variieren die Emigrationsraten von Kolonie zu Kolonie zwischen 0 und 25%. In einigen Fällen schienen Abwanderungen nicht spontan zu geschehen, sondern durch Umweltfaktoren wie ungünstige Klimabedingungen im Quartier ausgelöst zu werden. Größere Kolonien schienen mehr Mitgliedern benachbarter Kolonien bekannt zu sein als kleinere.

Literature

Arlettaz, R. (1995): Ecology of the sibling mouse-eared bats (*Myotis myotis* and *Myotis blythii*): Zoogeography, niche, competition, and foraging. Martigny: Horus Publishers.

Audet, D. (1992): Roost quality, foraging and young production in the mouse-eared bat *Myotis myotis*: A Test of the ESS model of group size selection. Ph.D. diss., York Univ., Ontario.

Bilo, M. (1990): Verhaltensbeobachtungen in einer Wochenstube des Mausohrs, *Myotis myotis* (Borkhausen, 1797). Nyctalus (N. F.) **3**, 99–118.

Braun, M. (1989): Bemerkungen zu einer Wochenstube von Mausohrfledermäusen, *Myotis myotis* (Borkh., 1797) in Nordbaden, FRG. In: European Bat Research 1987. Ed. by V. Hanák, I. Horácek, and J. Gaisler. Praha: Charles University Press. Pp. 527–531.

Eisentraut, M. (1960): Die Wanderwege der in der Mark Brandenburg beringten Mausohren. Bonner zool. Beitr. **11**, 112–123.

Felten, H.; Klemmer, K. (1960): Fledermausberingung im Rhein-Main-Lahn-Gebiet 1950–1959. Bonner zool. Beitr. (Sonderheft) **11**, 116–188.

Findley, J. (1993): Bats: a community perspective. Cambridge: Cambridge Univ. Press.

Gaisler, J.; Hanák, V. (1969): Ergebnisse der zwanzigjährigen Beringung von Fledermäusen (Chiroptera) zn der Tschechoslowakei: 1948–1967. Acta scien. natur. Brno **3**, 1–33.

Gebhard, J.; Ott, M. (1985): Etho-ökologische Beobachtungen an einer Wochenstube von *Myotis myotis* (Borkh., 1797) bei Zwingen (Kanton Bern, Schweiz). Mitt. Naturf. Ges. Bern (N. F.) **42**, 129–144.

Haensel, J. (1974): Über die Beziehung zwischen verschiedenen Quartiertypen des Mausohrs, *Myotis myotis* (Borkhausen 1797), in den brandenburgischen Bezirken der DDR. Milu **3**, 542–603.

Hanák, V. (1989): Bat-banding in Czechoslovakia: Results of 40 years of study: (1948–1987). In: European Bat Research 1987. Ed. by V. Hanák, I. Horácek, and J. Gaisler. Praha: Charles Univ. Press. Pp. 620.

Heidinger, F.; Vogel, S.; Metzner, W. (1989): Thermoregulatory behaviour in a maternity colony of *Myotis myotis.* In: European Bat Research 1987 Ed. by V. Hanak, I. Horacek, and J. Gaisler; Praha: Charles Univ. Press. Pp. 189–190.

Henkel, F.; Tress, C.; Tress, H. (1982): Zum Bestandsrückgang der Mausohren (*Myotis myotis*) in Südthüringen. Nyctalus (N. F.) **1**, 453–471.

Horácek, I. (1985): Population ecology of *Myotis myotis* in central Bohemia (Mammalia: Chiroptera). Aeta Universitas Carolinae – Biologica **8**, 161–267.

Hurka, L. (1988): Zur Verbreitung und Bionomie des Mausohr (*Myotis myotis*, Mammalia: Chiroptera) in Westböhmen. Folia Mus. Rer. Nat. Bohem. **27**, 33–55.

Müller, A.; Güttinger, R.; Graf, M. (1992): Steinmarder (*Martes foina*) veranlassen Große Mausohren (*Myotis myotis*) zur Umsiedlung. Artenschutzreport **2**, 14–17.

Oldenburg, W.; Hackethal, H. (1989): Zur Bestandesentwicklung und Migration des Mausohrs, *Myotis myotis* (Borkhausen, 1797), in Mecklenburg. Nyctalus (N. F.) **2**, 501–519.

Palmeirim, J.; Rodrigues, L. (1995): Dispersal and philopatry in colonial animals: The case of *Miniopterus schreibersii.* Symp. Zool. Soc. London **67**, 219–231.

Roer, H. (1968): Zur Frage der Wochenstuben-Quartiertreue weiblicher Mausohren (*Myotis myotis*). Bonn. zool. Beitr. **19**, 85–96.

Roer, H. (1988): Beitrag zur Aktivitätsperiodik und zum Quartierwechsel der Mausohrfledermaus *Myotis myotis* (Borkhausen, 1797) während der Wochenstubenperiode. Myotis **26**, 97–107.

Rogée, E.; Lehmann, G. (1994): Beobachtungen zur Biologie und Ursachen der Jugendsterblichkeit beim großen Mausohr in Nordhessen. In: Die Fledermäuse Hessens. Ed. by Arbeitsgemeinschaft für Fledermausschutz in Hessen. Remshalden: Manfed Henneke Verlag. Pp. 121–127.

Rudolph, B. U.; Liegl, A. (1990): Sommerverbreitung und Siedlungsdichte des Mausohrs *Myotis myotis* in Nordbayern. Myotis **28**, 19–38.

Tuttle, M. D. (1976): Population ecology of the Gray bat (*Myotis grisescens*): Philopatry, timing and patterns of movement, weight loss during migration, and seasonal adaptive strategies. Occ. Pap. Mus. Nat. Hist. Univ. Kansas **54**, 1–38.

Zahn, A. (1995): Populationsbiologische Untersuchungen am Großen Mausohr (*Myotis myotis*), diss. thesis, Ludwig-Maximilians Univ. München.

Zahn, A.; Dippel, B. (1997): Male roosting habits and mating behaviour of *Myotis myotis*, J. Zool. (London) **243**, 659–674.

Zöfel, P. (1992): Statistik in der Praxis. 3. Aufl. Stuttgart, Jena: Gustav Fischer.

Authors' address: Dr. Andreas Zahn, Zoologisches Institut, Universität München, Postfach 20 21 36, D-80021 München, Germany